In marked contrast, around 16,000 species within the 650–700 genera of legumes have been identified as forming nitrogen-fixing symbioses with rhizobia. If such diversity is taken as a measure of evolutionary success or fitness, the legume family within the Fabales has been considerably more successful than any other family of nodulating plants in the closely-related orders. Why is it that nitrogen-fixing nodules on legumes should appear to confer so much benefit compared with the non-legume nodulating plants? One clear difference is the different bacteria that infect them. Possibly *Frankia* spp. are less efficient at fixing nitrogen than rhizobia. However, the wide diversity of rhizobia that can nodulate plants suggests that successful nitrogen-fixing symbioses can be established by very diverse bacteria, even between different divisions of the bacteria. It is not apparent why *Frankia* spp. did not evolve a symbiosis that was as mutually beneficial (based on relative evolutionary diversity) as that seen with rhizobial-legume symbioses.

The difference in the structures of legume nodules compared with non-legume nodules may give an insight into why legume nodules are so successful. Nodules on non-legumes are somewhat similar to short modified lateral roots with a central vasculature. In contrast, legume nodules have a peripheral vasculature. A clear advantage of a peripheral vasculature is that oxygen will be available for energy production by mitochondria associated with the vasculature, and so ATP generated by respiration would be readily available to drive the energy demands of the vasculature. This would not normally be a significant problem in roots, but in a nodule with a central vasculature, the haemoglobin in the cells surrounding the vasculature would tend to bind most of the available oxygen. I propose that a physiological limitation on nodules with a central vasculature could be the relative difficulty of respiration, and hence ATP synthesis in the cells of the vasculature. The identification of a gene (*COCHLEATA* in pea and *NOOT* in *M. truncatula*) that normally represses root identity in nodules may be the first step toward identifying how legumes differentiate a peripheral vasculature.

Other reasons for the relative efficiency of legume nodules could be related to the genome duplications that occurred in some of the legume families. These duplications could have enabled the acquisition of additional evolved functions in duplicated genes, to help develop the highly efficient nitrogen-fixing nodules in current legumes.

## Further reading

Couzigou, J-M., Zhukov, V., Mondy, S., Abu el Heba, G., Cosson, V., Ellis, T.H.N., Ambrose, M., Wen, J., Tadege, M., Tikhonovich, I., et al. (2012). *NODULE ROOT* and *COCHLEATA* maintain nodule development and are legume orthologs of *Arabidopsis BLADE-ON-PETIOLE* genes. Plant Cell *24,* 4498–4510.

Desbrosses, G.J., and Stougaard, J. (2011). Root nodulation: a paradigm for how plant-microbe symbiosis influences host developmental pathways. Cell Host Microbe *10*, 348–358.

Downie, J.A. (2010). The roles of extracellular proteins, polysaccharaides and signals in the interaction of rhizobia with legume roots. FEMS Microbiol. Rev. *34,* 150–170.

Gutjahr, C., and Parniske, M. (2013). Cell and developmental biology of arbuscular mycorrhiza symbiosis. Annu. Rev. Cell Dev. Biol. *29,* 593–617.

Hayashi, T., Shimoda, Y., Sato, S., Tabata, S., Imaizumi-Anraku, H., and Hayashi, M. (2014). Rhizobial infection does not require cortical expression of upstream common symbiosis genes responsible for the induction of calcium spiking. Plant J. *77,* 146-159.

Miller, J.B., Pratap, A., Miyahara, A., Zhou, L., Bornemann, S., Morris, R.J., and Oldroyd, G.E. (2013). Calcium/calmodulin-dependent protein kinase is negatively and positively regulated by calcium, providing a mechanism for decoding calcium responses during symbiosis signaling. Plant Cell *25*, 5053–5066.

Morieri, G., Martinez, E.A., Jarynowski, A., Driguez, H., Morris, R., Oldroyd, G.E.D., and Downie, J.A. (2013). Host-specific Nod-factors associated with *Medicago truncatula* nodule infection differentially induce calcium influx and calcium spiking in root hairs. New Phytol. *200*, 656–662.

Mortier, V., De Wever, E., Vuylsteke, M., Holsters, M., and Goormachtig, S. (2012). Nodule numbers are governed by interaction between CLE peptides and cytokinin signaling. Plant J. *70*, 367–376.

Oldroyd, G.E.D. (2013). Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. Nat. Rev. Microbiol. *11*, 252–263.

Oldroyd, G.E.D., Murray, J.D., Poole, P.S., and Downie, J.A. (2011). The rules of engagement in the legume-rhizobial symbiosis. Annu. Rev. Gen. *45,* 119–144.

Santi, C., Bogusz, D., and Franche, C. (2013). Biological nitrogen fixation in non-legume plants. Ann. Bot. *111*, 743–767.

Singh, S., Katzer, K., Lambert, J., Cerri, M., and Parniske, M. (2014). CYCLOPS, a DNA-binding transcriptional activator, orchestrates symbiotic root nodule development. Cell Host Microbe http://dx.doi.org/10.1016/j.chom.2014.01.011.

Soyano, T., Kouchi, H., Atsuko, H., and Hayashi, M. (2013) NODULE INCEPTION directly targets *NF-Y* subunit genes to regulate essential processes of root nodule development in *Lotus japonicus.* PLoS Genet. *9*, e1003352.

Udvardi, M., and Poole, P.S. (2013). Transport and metabolism in legume-rhizobia symbioses. Annu. Rev. Plant Biol. *64,* 781–805.

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# Rank influences human sex differences in dyadic cooperation

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Unrelated human males regularly interact in groups [1], which can include higher and lower ranked individuals. In contrast, from early childhood through adulthood, females often reduce group size in order to interact with only one individual of equal rank [1–5]. In many species, when either sex maintains a group structure, unrelated individuals must cooperate with those differing in rank [6]. Given that human males interact more than females in groups, we hypothesized that dyadic cooperation between individuals of differing rank should occur more frequently between human males than females. We examined this hypothesis in academic psychology. Numbers of co-authored peer-reviewed publications were used as an objective measure of cooperation, and professorial status as a measure of rank. We compiled all publications co-authored by full professors with same-sex departmental colleagues over four years in 50 North American universities, and calculated the likelihood of co-authorship in relation to the number of available professors in the same department (Supplemental information). Among those of equal status (full professors) there was no gender difference for likelihood of co-authorship: women and men were equally likely to co-author publications with another full professor of the same gender. In contrast, male full professors were more likely than female full professors to co-author publications with a same-gender assistant professor. This is consistent with a tendency for men to cooperate more than women with same-sex individuals of differing rank.

We first tabulated the mean numbers of female full professors (M = 5.28), male full professors (M = 9.50), female assistant professors (M = 3.84) and

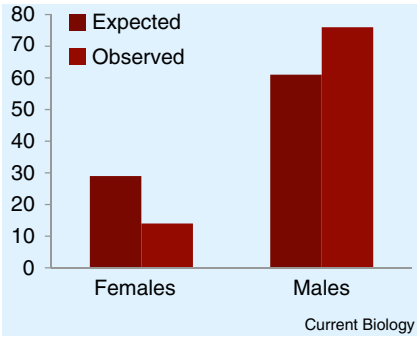


Figure 1. Sex differences in human cooperation.
Observed and expected numbers of publications with same-sex senior and junior colleagues. Female full professors published less frequently than male full professors with same-sex assistant professors in the department than would be expected by chance.

male assistant professors (M = 3.66) across 50 major institutions from 50 different states or provinces. The overall proportion of female full professors (35.7%) in this sample resembled the number cited for the field in 2006 in the United States (29.7%) [7].

We next tallied the total number of publications (N = 369) between two same-gender full professor co-authors within the same department for females (N = 58), and for males (N = 311). As our model applies only to dyadic cooperation, we did not include publications with more than two co-authors from the same department in any of our analyses. (There were 17 publications with more than two full professor co-authors and eight publications with two full professor and one assistant professor co-authors. Results remained unchanged when these were included.)

We then calculated the expected distribution of 369 same-gender co-authored publications if these directly reflected the number of unique combinations of same-gender pairs of senior (full professor) females and males. As the number of publications varied widely between departments (between 1 and 496), we first calculated mean numbers of female and of male pairs across departments, weighted by the total number of publications per department. This gave weighted mean numbers of senior female dyads (F = 11.93) and senior male dyads (M = 56.07). Numbers of unique pairs of senior female dyads, F*(F-1)/2, and senior male dyads, M*(M-1)/2, were calculated for each department. These were used to determine the expected values of the distribution of the 369 publications, rounded to nearest whole number (senior female co-authors: E = 65, senior male co-authors: E = 304). The actual distribution of co-authored publications between same-gender full professors did not differ significantly from the expected distribution, $\chi^2$ (1) < 1. In other words, the number of publications between two senior females and between two senior males closely paralleled the mean number of possible dyadic combinations of female and male full professors.

We next tabulated the number of co-authored publications between one senior female and one junior (assistant professor) female (N = 14) and one senior male and one junior (assistant professor) male (N = 76). As before, we calculated combinations of unique pairs of one senior and one junior of the same gender for each department and calculated the mean weighted by the number of publications. This gave weighted mean numbers of senior with junior female dyads (M = 21.70) and senior with junior male dyads (M = 46.22), which were used to determine the expected values of the distribution of the 90 publications, rounded to nearest whole number (female senior with female junior co-author: E = 29, male senior with male junior co-author: E = 61). There were significantly fewer publications co-authored by one senior female with one junior female than by one senior male with one junior male than would be expected, $\chi^2$ (1) = 11.45, $p < 0.001$ (Figure 1). In contrast, analysis of co-authored publications between senior and junior co-authors of the other gender (senior female and junior male: N = 19, E = 17; senior male and junior female: N = 28, E = 30) yielded no difference, $\chi^2$ (1) < 1. These results show that high-ranked male professors co-published more than high-ranked female professors with same-gender low-ranked faculty. No gender differences were obtained when comparing publications with other senior professors or when comparing senior professors with other-gender junior professors.

Our results are consistent with observations suggesting that social structure takes differing forms for human males and females. Males' tendency to interact in same-gender groups makes them more prone to cooperation with asymmetrically ranked males. In contrast, females' tendency to restrict their same-gender interactions to equally ranked individuals make them more reluctant to cooperate with asymmetrically ranked females.

The present study does not demonstrate whether the reduced level of cooperation among women of different status is due to higher-ranked or lower-ranked women. However, our findings are consistent with results from early childhood onwards suggesting that females of lower status can be uncomfortable cooperating with their superiors [4,5]. Female superiors may also be less willing than male superiors to invest in lower-ranked same-sex individuals. These sex differences would not be expected to exist in the same way in collaborations between professors and their students, who will typically take positions at other institutions and hence not compete as directly. This study refines research on sex differences in adult cooperation during economic games [8] by demonstrating that rank differentials constitute an important factor.

## Supplemental Information

Supplemental Information including experimental procedures can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.12.047.

## References

1. Markovits, H., Benenson, J., and Dolenszky, E. (2001). Evidence that children and adolescents have internal models of peer interactions that are gender differentiated. Child Dev. *72*, 879–886.
2. Eder, D., and Hallinan, M. (1978). Sex differences in children's friendships Am. Sociol. Rev. *43*, 237–220.
3. Benenson, J.F. (1993). Greater preference among females than males for dyadic interaction in early childhood. Child Dev. *64*, 544–555.
4. Benenson, J.F. (2013). The development of human female competition: allies and adversaries. Phil. Trans. Roy. Soc. B *1631*, 20130079.
5. Eagly, A.H., and Karau, S.J. (2002). Role congruity theory of prejudice toward female leaders. Psychol. Rev. *109*, 573–598.
6. Kappeler, P., and van Schaik, C. (2006). Cooperation in Humans and Primates: Mechanisms and Evolution. (New York, NY: Springer).
7. Rosser, S.V. (2012). Breaking Into the Lab: Engineering Progress for Women in Science (New York, NY: New York University Press).
8. Balliet, D., Li, N.P., Macfarlan, S.J., and Van Vugt, M. (2011). Sex differences in cooperation: A meta-analytic review of social dilemmas. Psychol. Bull. *137*, 881–909.

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